tion within the complex genus *Sorghum,* especially in the subgenera *Para-Sorghum* and *Stiposorghum.*

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Division of Genetics,
University of California, Berkeley,
and Department of Plant Sciences,
University of Oklahoma, Norman.

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EVIDENCE FOR THE HYBRID NATURE OF X LIATRIS CREDITONENSIS

L. O. Gaiser

This paper[1] is concerned with a plant described by the author (1946) as a putative hybrid between *Liatris ligulistylis* and *L. squarrosa* var. *glabrata,* under the name of × *L. creditonensis.* Because of the practical difficulty of controlled breeding of Compositae, it has not been possible to demonstrate the hybrid nature of × *L. creditonensis* by planned resynthesis. The available evidence that it is a hybrid is here presented.

Liatris ligulistylis (Nels.) K. Sch. has a known range of the three prairie provinces of western Canada and southward along the eastern side of the Rocky Mountains through western South Dakota, Wyoming, and Colorado into northern New Mexico. It favors comparatively moist habitats. *Liatris squarrosa* (L.) Michx. var. *glabrata* (Rydb.) Gaiser on the otherhand is found on the dry open plains from Kansas to South Dakota. The ranges of these two entities do not overlap.

A garden plot of thirty-two plants of *L. squarrosa* var. *glabrata* (Accession No. 9) planted in 1928 from seed collected in Nebraska (high cliff northwest of Royal, Antelope County, 4 October 1927, *Wernicke*) developed into uniform, one-stemmed plants during their second year of growth, and by 1933 when they were five years old they had become several stemmed (Pl. 1, fig. 1). Growing beside this plot were two plants of *L. ligulistylis* (Acces-

[1] The author is indebted to Dr. R. Rollins and E. Anderson for reading the manuscript and to the latter also for suggesting Fig. 2.

sion No. 1) which had been collected in Minnesota (near Erskine, Polk County, August, 1929, *Gaiser*). One was atypical in being more paniculate and in having more elongated basal peduncles than is usual in the species (Pl. 1, fig. 2).

Although stray seedlings were normally weeded out from the plots, one which was growing at the side of the bed of *L. squarrosa* var. *glabrata* and next to the two plants of *L. ligulistylis* was allowed to persist. In 1932 this plant (No. 52) bloomed and was seen to be intermediate between those two entities (Table 1), although the influence of *L. squarrosa* was more pronounced. This plant (Pl. 1, fig. 3) proved to be the supposed hybrid, × *L. creditonensis.*

Because phyllaries show a wide variation in form and were considered important in distinguishing closely related species within a series, it was hoped that from the recombinations of their characters in this plant (No. 52), some knowledge of its parentage might be gained. In the phyllaries of plant No. 52, the characters of *L. ligulistylis* and *L. squarrosa* var. *glabrata* were combined even more that it was possible to indicate in Table 1.

Cytological Observations

Chromosome counts from pollen mother cells of *L. squarrosa* var. *glabrata* (No. 9) were $n = 10$ (fig. 1 a–d) and from seedling root tips, $2n = 20$. Meiotic figures (fig. 1, e, f) of *L. ligulistylis* (No. 1) appeared very similar to those of *L. squarrosa* var. *glabrata.* In the putative hybrid (No. 52) first metaphase plates showed ten chromosomes (fig. 1, g, h). A study of numerous lateral and polar first metaphase figures showed that there was always regular pairing of the bivalents. The anaphase and telophase proceeded regularly; at second metaphase (fig. 1, i, j), the uniformity of the chromosome plates was striking. There were no lagging chromosomes; second telophases and pollen tetrads were perfectly formed. Because of the similarity of the meiotic chromosomes of the two putative parental species, however, the form and number of the chromosomes was of little help in determining the origin of seedling No. 52.

Progeny of × L. creditonensis No. 52

The putative hybrid (No. 52) was partially fertile when open-pollinated. A number of achenes were obtained the first year that the plant was observed in bloom. Since the seeds were sown late in the season, many of the seedlings did not have time to develop a sufficiently thick corm to survive the winter. Thus, the fact that only fifteen strong seedlings were available for transplanting in the spring is not necessarily indicative of the vitality of the lot.

In September 1934, the seedlings were in their second year and most of them had come into bloom. Two of them with narrower, more rigid, declined and somewhat twisted rather than broader upright leaves, and with projecting phyllaries were very much like *L. squarrosa.* Three of them more closely resembled the parent plant No. 52 in their wider, somewhat erect leaves. However, these three were not alike in their phyllaries, two of them again having the more outspread phyllaries like *L. squarrosa* and one having phyllaries similar to those of its parent. Thus, progeny of the putative hybrid showed various recombinations of the characters of *L. squarrosa* and *L. ligulistylis.*

With regard to seven characters, the progeny were compared with the seed parent and with the two original species. Most of the progeny were nearly like the seed parent. Three were quite like *L. squarrosa,* and eight more approached *L. squarrosa* in one character or another. None closely resembled *L. ligulistylis.*

At various times during the study, voucher specimens for deposit in the Gray Herbarium were taken from × *L. creditonensis,* from the putative parents and from the various progeny.

Cytological Examination of Progeny of Plant No. 52

Meiosis was studied in the pollen mother cells of one resembling *L. squarrosa* and of another resembling the seed parent. In both, divisions were normal with a regular arrangement of ten bivalents at first metaphase (fig. 1, k, l). Though many clear figures of all stages of the first and second divisions were seen, no lagging units on the spindles and no micronuclei were found. One count of eleven chromosomes on a second metaphase plate suggested irregularities (fig. 1, n) but was probably due to precocious splitting of one chromosome or to pressure on the mount. Slight pressure on the coverslip over first metaphase plates caused a similar elongation of a few of the bivalents as they were seen somewhat laterally (fig. 1, m). Study of a third plant during two different seasons showed only mature pollen which was very regular in form.

In 1934 seven of the progeny produced many good achenes, though one produced only six. From each of the seven, fifteen achenes were germinated for cytological examination of the root tips. The percentage of germination was good, varying from 40 to 86 in all except one which was not tested at the same time as the others and for which it was believed that temperature conditions were unfavorable. Of the plant which produced six achenes, all except one germinated. In 1935, achenes were col-

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Explanation of the Figures, Plate 1.

Plate 1. Specimens of Liatris Grown in Garden. Fig. 1, Five year old seedling of *L. squarrosa* var. *glabrata* (No. 9 plant 32).—Fig. 2, *L. ligulistylis* (No. 1 plant 2).—Fig. 3, × *L. creditonensis* (No. 52) photographed 1933. All approximately × 1/7.

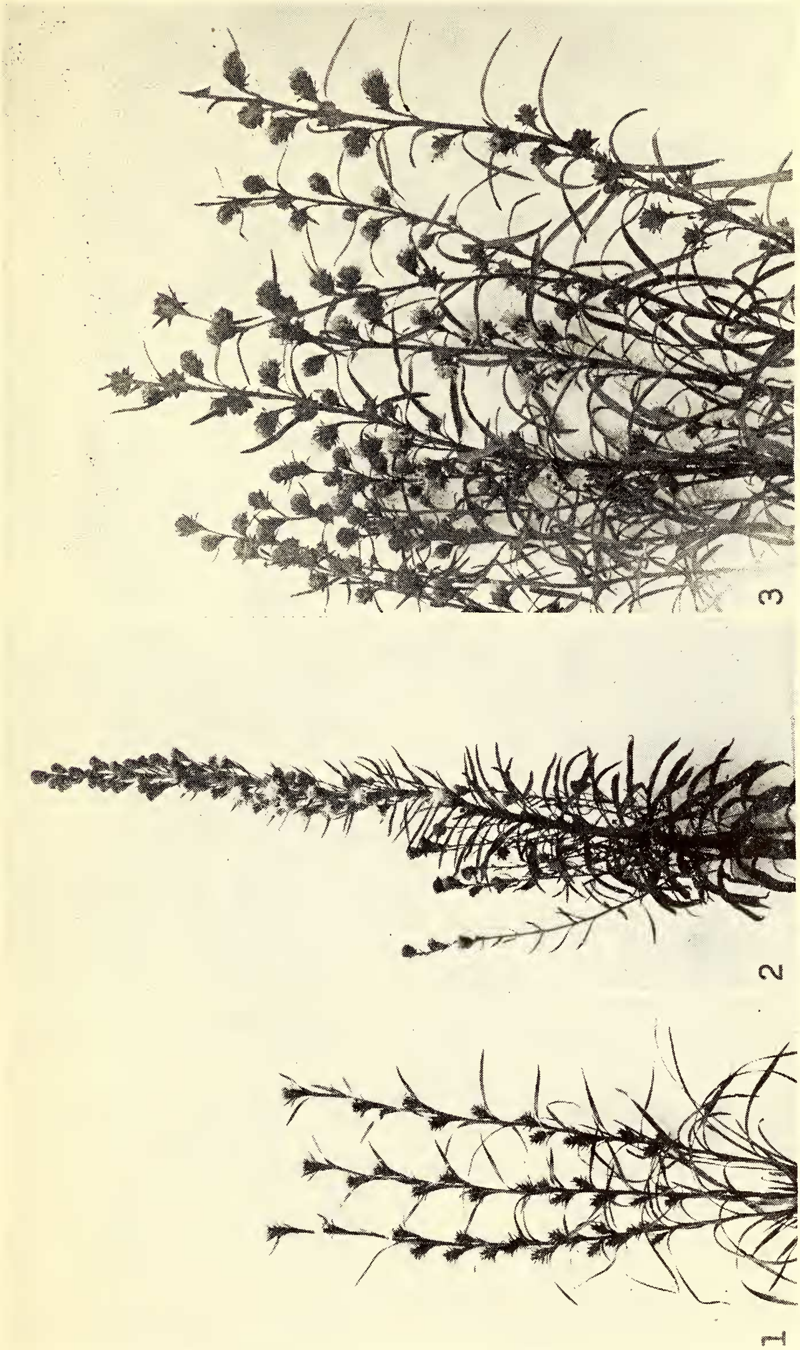

PLATE 1. SPECIMENS OF LIATRIS GROWN IN GARDEN.

TABLE 1. COMPARISON* OF LIATRIS HYBRID WITH PUTATIVE PARENTS

	L. squarrosa var. *glabrata* No. 9	*L. ligulistylis* No. 1	× *L. creditonensis* No. 52
Corolla			
Color**	Mathews purple, 65	Lilac, 65d.	Lilac, 65d.
Length	12mm.	7-9mm.	9mm.
Shape	Erect to end of pappus and then flattened (rotate)	Erect, tubular	Erect, tubular
Lobes	Hairy	Glabrous	Slightly hairy
Style			
Length	20mm.	14mm.	18mm.
Color**	Mauvette, 65f.	Lilac, 65d.	Mauvette, 65f.
Pappus			
Length	7mm.	7-8mm.	8mm.
Nature	Plumose	Barbellate	Barbellate
Achene			
Length	6mm.	4-5mm.	6mm.
Phyllaries			
Color	All green	Green with reddish tips	All green
Nature	Glabrous, chaffy	Glabrous, membranous	Glabrous, not quite as chaffy as #9
Margin	No cilia, not scarious	Markedly scarious and lacerate	No cilia, not scarious
Position	Outspread	Erect, very slightly incurved	Mostly slightly incurved
Shape of outer ones	Sharply acuminate 	Broadly ovate and short 	Elliptical acute, not sharply acute 
Size of outer ones	12mm. long	4-5mm. long	10-11mm. long, 3-4mm. wide
Shape of inner ones	Linear acute 	Broadly spatulate 	Linear, spatulate 
Length of inner ones	15mm. long	8mm. long	15mm. long
Peduncles	4-8mm. long	4mm.-12cm. (of basal flower)	20-25mm. long

* These observations were made at the time the styles were exserted, August 1933, with revision of pappus and achene lengths to those of mature conditions.
** Colors are according to Ridgway's Color Chart, plate XXV.

lected from eleven plants, of which five were other than those checked in the previous season. Though their viability was not tested, it is probable from the appearance of the well-filled achenes that their germination would have been as high. The somatic chromosome number was confirmed as twenty in six seedlings.

In numerous figures obtained from one seedling, at least two pairs of chromosomes were found to be longer than the rest, one pair long-median, and one pair sub-median. For the rest of the chromosomes, it was difficult to draw a line between those of intermediate length and the shortest ones.

Further Analyses of the Progeny

Using the hybrid index method of Anderson (1949), × *L. creditonensis* was compared with its putative parents and with its

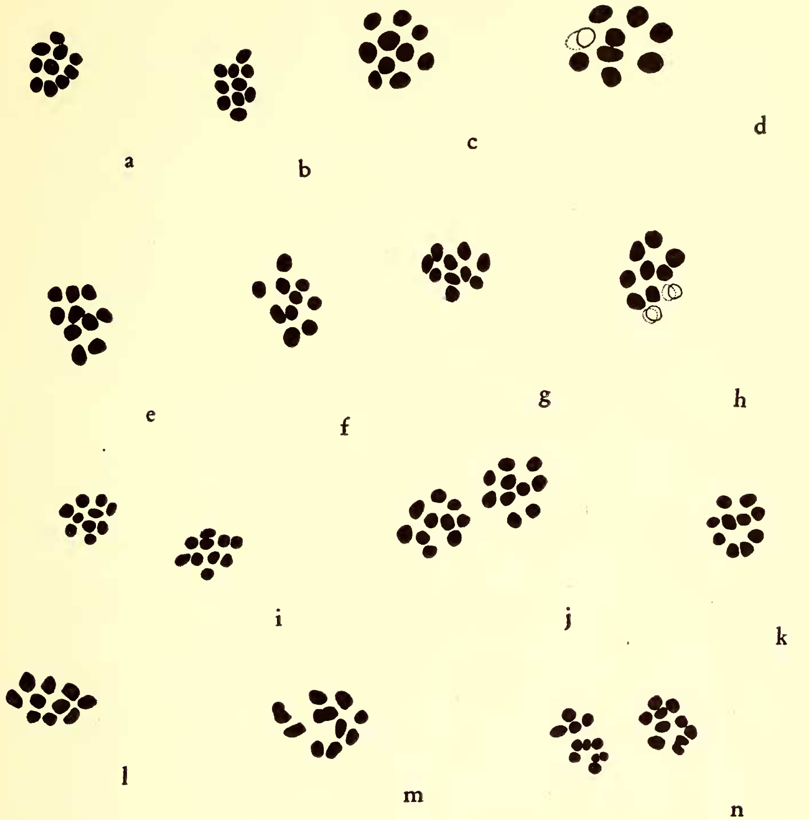

FIG. 1. Meiotic chromosomes of × *L. creditonensis* and the two putative parents as seen in polar views of first metaphase (except i, j, n which are second metaphase) in pollen-mother-cells from aceto-carmine preparations, drawn by Zeiss apochromatic lenses and camera lucida at aproximately ×1900. FIGS. a–d, *L. squarrosa* var. *glabrata* No. 9 ($n = 10$): *a, b,* two young seedlings in their first summer of bloom; *c, d,* seedling 32 in its fifth year. FIGS. e, f, *L. ligulistylis* No. 1 plant 1 ($n = 10$). FIGS. g–j, × *L. creditonensis* No. 52 ($n = 10$): *g,* drawn in 1932; *h–j* drawn in 1933. FIG. k, plant 8 of progeny of No. 52. FIGS. l, n, plant 12 of progeny of No. 52.

progeny, nine diagnostic and measurable characters being studied from the herbarium material—pilosity of corolla limb; nature of the pappus (length of barbules); margin, shape, and position of phyllaries; shape, surface, and margin of leaves; and pubescence of upper stem (Table 3).

As to the first character considered, pilosity of the corolla limb, *L. squarrosa* has hairy corolla lobes, whereas *L. ligulistylis* has a completely clear corolla, lacking any pilosity within the limb, throat, or tube. This is in contrast not only to *L. squarrosa,* but also to other species of the *Scariosae* which have hairs within the throat. (In referring to parts of the corolla, the tube proper will here be regarded as the part below the insertion of the filaments, the part above that being referred to as the throat and limb, of which the latter refers to the teeth only.) In determining the hybrid index, *L. squarrosa*, with profuse hairs, was scored 4, × *L. creditonensis*, with few hairs, 1, and *L. ligulistylis*, with no hairs, 0. The progeny was scored from 1 to 4.

The second character considered was nature of the pappus. *L. squarrosa* has a very plumose pappus, whereas in *L. ligulistylis* the pappus is barbellate and to the naked eye not obviously plumose. As can be seen in those species of *Liatris* having a plumose pappus, the barbules toward the base of the seta are generally shorter. Also, as was noticed early by Cassini (1827) in *Suprago*, even along the mid portion of the seta there are differences in length of the barbules. Inasmuch as only the longest projecting barbules are readily distinguishable when setae are flattened under a cover slip, measurements were made only of these longer barbules. The figures, therefore, do not represent the full range of length. For each species, measurements were made of ten specimens from widely distributed localities. These included the isotypes and two plants of each of the accessions studied above. For each of these plants, twenty-five barbules were measured. In making these preparations, it was found that lactic acid was a satisfactory mounting medium for the short-barbuled setae of *L. ligulistylis*, but for the plumose setae of *L. squarrosa* parlodion proved to be better. Table 2 gives the means and standard errors of these measurements. Plant No. 52 falls between the two species, just at the upper limits of *L. ligulistylis*. This confirms the macroscopic determination of its pappus as barbellate (Gaiser, 1946). Only one of the progeny had a mean lower than that of the parent plants, and the rest fell between it and *L. squarrosa*. In determining the hybrid index, the barbule length of *L. ligulistylis* was scored as 0 and that of *L. squarrosa* as 2. Intermediate lengths were then scored fractionally.

For the other eight measurable and diagnostic characters studied, the condition of *L. ligulistylis* was scored 0, the intermediate condition 1, and the condition of *L. squarrosa* 2, except for pilosity of corolla limb which was scored from 0 to 4. Scoring and totals are shown in Table 3. Thus, with the putative parents having a total score of 0 and 20, plant No. 52 receives only a total of 10.44. The scores of the progeny fell between those of *L. squarrosa* and × *L. creditonensis*, the highest nearly approaching that of *L. squarrosa* and the lowest that of × *L. creditonensis*, none approaching closely to *L. ligulistylis*. This confirms the observations on the living plants, most being like the parent plant or intermediate between the latter and *L. squarrosa*. Independent segregation is shown, however, in some of the charac-

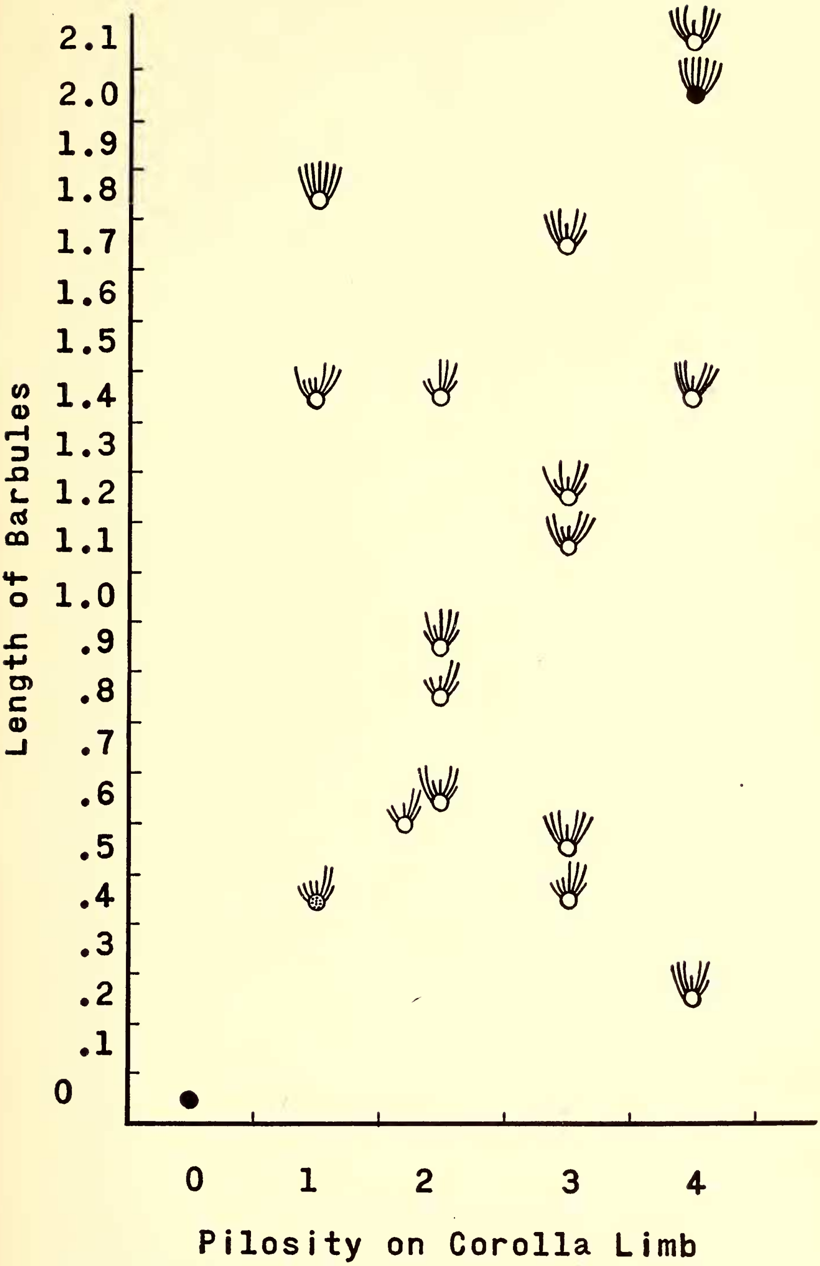

FIG. 2. Scatter diagram of progeny of × *L. creditonensis* (Plant No. 52): *L. ligulistylis* (black circle in lower left); *L. squarrosa* (black circle in upper right); *L. creditonensis* (stippled circle); the progeny (clear circles). From left to right the symbol arms represent the phyllary, leaf and stem characters in Table 3, long arms a score of 2, and half length, a score of 1.

ters. In the pictorialized diagram (fig. 2), the diversity of the progeny is at once apparent. On the basis of the characters scored, no two of them are exactly alike.

Discussion

With the common observation of the intermediacy of an F_1 between the two parents, it is sometimes less well remembered how greatly the progeny of even an F_2 vary from one another. However, as Anderson (1949) has recently emphasized, the number of recombinations in an F_2 is not numerous considering the total possibilities in the multitudinous characters of two species. Because of the linkage of genes, as at least one limiting factor, fewer types of combination are achieved. Also as he has pointed out from the analysis of hybrid populations under natural conditions, there is a repeated backcrossing of the hybrids to one or both of the parents, and with each successive generation the hybrid nature is less apparent. The result is that a few resemble the recurrent parent and a few the F_1, but a larger proportion will be intermediate between these two.

In Plant 52 (× *Liatris creditonensis*) and its progeny, there was shown a change from the distinct intermediate plant No. 52 to some of its progeny. Because of the failure of some of the insufficiently developed seedlings to over-winter, the complete population could not be represented in the study. The fifteen progeny which were grown varied so slightly among themselves that when for lack of better characterization they were divided into seven categories, two were described as practically like the parent plant and eight were considered close to it but with other combinations of characters from the one contributing parent species *L. squarrosa*. While two categories were recorded at that time based on close similarity to *L. squarrosa*, none pointed singly to *L. ligulistylis*. The more extended analysis (Table 3), including measurements of two characters of a quantitative nature, confirm this. Though the total scores of the progeny range from those very nearly as low as the parent plant No. 52 to those very nearly as high as *L. squarrosa*, none at all had a score approaching *L. ligulistylis*. These plants seem to meet the situation described by Anderson of a backcross to the recurrent parent with *L. squarrosa* as that parent. As there was quite a bed of *L. squarrosa* (No. 9) seedlings (originally there had been thirty-two) it is logical to assume that there would be more pollen of that species available for pollination than of *L. ligulistylis*, of which there were only two plants. Because the hybrid was open-pollinated it is not known whether the seeds that were germinated were really the result of fertilization of those flowers by pollen of other flowers of the same plant or by pollen of plants of either or both of the other two species. Compatability of the chromosomes of either species could be expected in view

TABLE 2. MEAN LENGTH OF BARBULES OF PAPPUS

Specimens examined		Barbule length	Standard Error
Liatris ligulistylis**		30.54	±.2820
Liatris squarrosa var. glabrata**		92.37	±.5235
X L. creditonensis, No. 52		43.85	±.8708
Progeny of No. 52	Plant 6	35.85	±.8799
	" 2	43.85	±.8032
	" 4	45.25	±.6349
	" 7	47.05	±1.2291
	" 15	47.25	±.8216
	" 1	53.25	±1.1080
	" 9	55.05	±.7525
	" 8	59.25	±.7362
	" 5	63.65	±1.0672
	" 11	65.65	±1.1256
	" 3	72.65	±1.1113
	" 12	72.65	±1.0745
	" 14	73.05	±1.1055
	" 10	86.25	±1.7644
	" 13	94.05	±1.0460

**Based on 250 measurements; the others each based on 25 measurements.

Mean barbule length in Table 2 given in micrometer spaces, 1 ocular micrometer space equaling 5.2 microns.

of the regular conjugation and divisions in the hybrid itself. Since morphologically as well as cytologically the seedlings qualify as successful backcrosses under natural conditions, a majority of these may have received the more abundant pollen of *L. squarrosa*.

Granted plant No. 52 is a hybrid, the regular pairing in meiosis of the pollen mother cells showed that the chromosomes of the two gametic genomes were homologous. If the chromosomes of the two contributing parents did not differ structurally they would have differed in their genic structure. Two such species which are not reproductively isolated, according to the classification of Mayr (1948), would be but subspecies. Also according to Clausen, Keck and Hiesey (1945), since their genetic systems were so balanced as to allow a free interchange without seriously impairing the ensuing development of the offspring, they would be classified as ecotypes of one species.

It is of interest to note that *L. ligulistylis* and *L. squarrosa* are species of the series *Scariosae* and *Squarrosae*.

On the basis of their barbellate or plumose pappus, Cassini (1827) placed these two series under the sections *Suprago* and *Euliatris,* respectively. Thus × *L. creditonensis* is an intersectional as well as interserial hybrid. Significant evidence of the hybrid origin of × *L. creditonensis* seems to lie in the measurements of the barbules of the pappus of the plants under consideration. As given above, the means of the lengths of barbules of the two putative parents were 30.54 and 92.37 and that of the hybrid was 43.85. Such a value is indeed a near intermediate as is generally found in the F_1 in quantitative characters, and the values of the progeny show recombinations expected in the next generation. It is known that when two pairs of factors affect a character (in multiple factor inheritance) the proportion of the F_2 progeny falling within the range of either parent equals $\frac{1}{16}$. For this one character of pappus, the values in the table suggest that such an interpretation might possibly be considered. *Liatris Weaveri* (Shinners, 1943), though it has not been reproduced experimentally, similiarly appears to represent an intersectional hybrid, between the series *Scariosae* and *Punctatae* (with plumose pappus).

The cytology of × *L. Weaveri* is being treated also (Gaiser, in press I). There are a number of examples in other plant genera of hybrids between what have been considered good allopatric species and even between genera. Therefore, such well recognized forms as *L. squarrosa* and *L. ligulistylis* surely fall into the category of generally recognized good species. Knowing what species were growing in the plot at the time of the appearance of × *L. creditonensis,* it is difficult to see what other parental sources could have given rise to it. Yet the final proof would lie in its experimental resynthesis. Other hybrids of this genus are being reported upon (Gaiser, in press II). Of the ten hybrids listed for the genus (Gaiser, 1946) six were intersectional hybrids. Also, in every series of the genus but two, the *Graminifoliae* and *Pauciflorae,* at least some species had been involved in such hybridization (Gaiser, 1950). According to the classification based on biosystematic principles (Clausen, Keck, and Hiesey), the several intersectional hybrids would seem to mean that much of the genus *Liatris* is one cenospecies.

As seen in plant No. 52, × *L. creditonensis* was a sucessful hybrid judged by the achene development and the high percentage of seed germination. The cytological observations foretold this condition in the regularity of meiosis and the formation of regular pollen grains. It was analyzed as a hybrid between *L. squarrosa* var. *glabrata* and *L. ligulistylis,* a hybrid between two species for which there is a natural barrier of geographic isolation. But when these two are brought together, hybridization can result.

TABLE 3. HYBRID INDEX OF PLANT NO. 52 AND ITS PROGENY

	Pilosity on Corolla Limb	Length of Barbules of Pappus	Phyllary			Leaf			Upper Stem	
			Margin	Shape	Position	Shape	Surface	Margin	Pubes-cence	Total
L. liguliststylis No. 1	0	0	0	0	0	0	0	0	0	0
L. squarrosa var. _glabrata_, No. 32	4	2	2	2	2	2	2	2	2	20
X. _L. creditonensis_ No. 52	1	.44	1	1	1	1	2	2	1	10.44
Progeny Plant, of No. 52 1	3	.75	2	2	2	1	2	2	2	16.75
2	3	.44	1	1	1	2	2	2	1	13.44
3	2	1.40	1	1	0	2	2	2	1	12.40
4	3	.49	2	2	2	1	2	2	2	16.49
5	3	1.10	2	2	1	1	2	2	2	16.10
6	4	.17	2	2	2	1	2	2	1	16.17
7	2	.55	2	2	1	1	2	2	1	13.55
8	2	.92	1	2	1	2	2	2	1	13.92
9	2	.81	1	1	0	1	2	2	1	10.81
10	1	1.85	2	2	2	2	2	2	2	16.85
11	3	1.17	2	1	2	1	2	2	1	15.17
12	1	1.40	2	1	1	1	2	2	2	13.40
13	4	2.11	2	2	2	1	2	2	2	19.11
14	4	1.41	2	2	2	1	2	2	2	18.41
15	2	.57	1	1	0	1	2	2	1	10.57

Summary

1. Two species of *Liatris* from different sections of the genus were grown in an experimental garden. A seedling appeared whose intermediacy, vigor, and breeding behavior indicated that it was a first generation hybrid between these two species.

2. There was no evidence of cytological irregularities or of any sterility either in the hybrid or its open-pollinated progeny.

3. Fifteen open-pollinated seedlings of the hybrid were raised to maturity and measured for a series of characters. They are as a whole intermediate between the hybrid and one of the parents, suggesting that wholly or in part they are back-crosses.

4. The concept of the cenospecies, as applied to *Liatris*, is discussed in the light of these results.

Biological Laboratories,
Harvard University,
Cambridge, Massachusetts

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MORTON EATON PECK

Morton Eaton Peck, Professor-Emeritus of Biology at Willamette University and dean of plant taxonomists in the Pacific Northwest, will celebrate his eightieth birthday on March 12, 1951.

Born in La Porte City, Iowa, Dr. Peck received most of his formal academic training at Cornell College (Iowa). After graduation he held several teaching posts in Missouri and Iowa and spent two fruitful years as a botanical collector in British Honduras. In 1908 he came from a professorship at Iowa Wesleyan to Willamette University, Salem, Oregon.

More than half of his eighty years have thus been spent in acquiring an unequaled knowledge of the natural history of